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Cellulose, lignin and nitrogen concentrations as rate regulating factors in late stages of forest litter decomposition

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With 3 Figures

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1. Introduction

The initial chemical composition of plant litter influences its decomposition rate as well as the chemical changes occurring during decomposition of that litter (Swift et al. 1979; Berg & Staaf 1980b). The organic-chemical constituents of litter can be divided into three broad groups, namely (1) soluble substances, (2) polymer carbohydrates or holocellulose, and (3) acid-insoluble aromatic compounds including lignin and phenolic decomposition products. Each group begins its net mass loss at a different stage of decomposition (Tenney & Waksman 1929; Mikola 1954; Berg et al. 1982a). The decomposition patterns of these groups differ among litter types, making it difficult to predict general decomposition patterns.

Lignin and related compounds are decomposed slowly, and studies have demonstrated that decay rates are often negatively correlated with lignin concentrations, both initially (Fogel & Cromack 1977; Melillo et al. 1982) and in later stages (Berg & Staaf 1980b). In addition, lignin disappearance is often slower in nitrogen-rich than in nitrogen-poor litters (Hermann et al. 1977; Berg et al. 1982b). In contrast, polymer carbohydrates are decomposed more rapidly, but because lignin and polymer carbohydrates are physically and chemically associated, neither group of compounds decomposes independently of the other.

The roles of organic-chemical composition and nutrient concentration of litter in determining decay rates remain unclear, especially for litter in later stages of decay. Our objective in this paper is to demonstrate how the composition of lignocellulose and the concentration of nitrogen affect litter and lignin mass loss rates in later stages of decomposition. We, therefore, developed a model based on decomposition data for Scots pine needle litter from one site and tested its validity with data of other litter types from two other sites. Finally, we tested the generality of our observations by combining data from several sites in contrasting ecosystems. A new model is proposed to describe the chemical regulation of decomposition in late stages of decay, using previously published data.

2. Site descriptions
2.1. Swedish sites (Jädraås and Malung)

The primary Scots pine (*Pinus sylvestris* L.) forest was 120 to 130 years old and located at the SWECON research site, near Jädraås, central Sweden (60°49′ N; 16°30′ E). The mean annual precipitation at a nearby village was 609 mm (1931—1960) and the mean annual temperature was +3.8 °C. The average actual evapotranspiration (AET) (Thornthwaite & Mather 1955, 1957)

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for the years 1974 to 1981 was 390 mm. The soil in the old Scots pine forest was a Spodosol with a well-developed A2-horizon (2—7 cm). The forest floor was a typical mor. More complete descriptions are given by AXELSSON & BRÅKENHIELM (1980) and BERG et al. (1982a). Decomposition studies were also carried out in a clear-cut area about 500 m from, and almost identical (before clear-cutting) to, the site described above.

Additional decomposition studies in Sweden were carried out in four Scots pine and four lodgepole pine (P. contorta DOUGL.) experimental plantations about 20 years old located in west-central Sweden close to the town of Malung (60°33′ N; 13°44′ E). These sites were more nutrient-rich than the Jädraås site. Average AET in 1978 to 1979 was 415 mm. No further site description is available.

2.2. Wisconsin site (Blackhawk Island)

The mixed-deciduous stand was located on Blackhawk Island in the Wisconsin River, south-central Wisconsin (43°38′ N; 89°47′ W). The 30-year mean annual temperature was +7.6 °C and the mean annual precipitation was 799 mm. AET was 606 and 599 mm for the incubation years of 1980/81 and 1981/82, respectively. Dominant vegetation was sugar maple (Acer saccharum MARSH.), occupying 50 % of the total basal area of 31 m^2 ha^{-1}. The canopy cover was dense and as a result the understory was sparse. There was no evidence of logging or other major disturbance.

The soil is a typic Hapludalf (Alfisol) with a mull forest floor. The site is relatively nutrient rich, with an estimated annual nitrogen mineralization rate of 125 kg N ha^{-1} a^{-1} (McCLAUGHERTY et al. 1985). The site is further described by PASTOR et al. (1982).

3. Materials and methods

3.1. Litter materials and incubations

Litter materials used in the Swedish study included Scots pine needles (collected in different years and from different sites), birch (Betula pubescens EHRH.) leaves, lodgepole pine needles, heather (Calluna vulgaris HULL) shoots, and cowberry (Vaccinium vitis-idaea L.) leaves. Brown foliage litter was collected in the autumn by shaking limbs gently and collecting the abscised foliage on tarpaulins spread beneath the trees. Heather shoots were cut, and recently dead cowberry leaves picked, from the plants.

Brown needle litter with different nutrient concentrations was collected in the autumns of 1975 and 1976 from 20-year-old Scots pine stands at Lisselbo. This site, an optimum nutrition experimental area described by TAMM et al. (1974), is situated about 50 km southeast of Jädraås on a sandy soil. Samples were taken from a control plot (N0) and from three plots (N1, N2, and N3) given different doses of ammonium nitrate.

Green needle litters of different nutrient concentrations were taken from branches of 20-year-old Scots pines grown at two sites. Samples were taken from the control plot of the fertilization experiment mentioned above (here called set P) and from the Jädraås site (sets M and O).

Collected materials were air dried, and samples weighing approximately 0.7 g were placed into 1-mm mesh terylene-net bags. Subsamples were retained for determination of initial moisture concentration and chemical analyses. Bags were distributed to 20 randomly located plots in each of the study sites and were held in place on the forest floor by metal pins. After various incubation periods, 20 bags were retrieved, their contents dried at 85 °C, weighed, milled to pass a 1-mm mesh sieve, and pooled for chemical analyses.

At the mature forest site at Jädraås, incubations of local Scots pine needles were started at least annually from 1974 to 1977 (sets A—E). In the autumns of 1975 and 1976 incubations of Scots pine needle litter of different nutrient concentrations (set 1 N0—N3 and set 2 N0—N3) were started (BERG & STAAF 1980b). In a nearby clear-cut area, local brown litter (set L) and local green needle litter (sets M and O), as well as transplanted needle litter (set P), were incubated beginning in May 1976 (BERG & EKBOHM 1983). Heather shoots were incubated in the old forest beginning in September 1977 and cowberry leaves beginning in October 1977 (BERG 1981). At the Malung site, local Scots pine and lodgepole pine needles were incubated beginning in May 1978 (BERG & LUNDMARK 1985).

Litter materials used at the Blackhawk Island site were white pine (P. strobus L.) needles, white oak (Quercus alba L.), and sugar maple leaves. Foliage litter was collected from a number of 1-x 30-m screens spread on the forest floor during the period of leaf fall in October 1980. Collected litter materials were air dried, and samples weighing approximately 4 g were placed in polyester litter bags with a mesh of 0.1 mm. Subsamples were retained for determination of initial moisture concentration and chemical analyses. Litter bags were randomly located within a permanently marked grid on the site beginning in November 1980. After various incubation periods, four bags per litter type were retrieved, their contents dried at 60 °C, weighed, and milled to a pass a 1-mm mesh sieve. Subsamples were taken for ash, moisture, and nitrogen determinations. The residuals of the samples were pooled for subsequent lignin and holocellulose analysis (ABER et al. 1984).

3.2. Chemical analyses

Chemical analyses for lignin and nitrogen were similar in the Sweden and Wisconsin studies but the methods for determination of solubles differed. Solubles were extracted from Swedish samples with water, followed by ethanol in a sonicator bath (BERG & STAAF 1980a). Soluble substances were extracted from Wisconsin samples with dichloromethane (Anonymous 1976), followed by hot water (Anonymous 1975). Cellulose and hemicelluloses were hydrolyzed in a two-stage digestion with sulfuric acid. The method of BETHGE et al. (1971) was used for the Swedish samples (see also BERG et al. 1982a) and the method of EFFLAND (1977) was used for Wisconsin samples. The residue of the sulfuric-acid hydrolyses was defined as sulfuric-acid (Klason) lignin.

Nitrogen analyses were performed on Swedish samples using a microkjeldahl procedure (NIHL-GÅRD 1971). Wisconsin samples were analyzed using a sulfuric acid-hydrogen peroxide digestion (MILLER & MILLER 1948) followed by analysis of ammonium with a Technicon Autoanalyzer (Anonymous 1977).

3.3. Comments on methods and terminology

Litter bags with different mesh sizes were used in the Jädraås and Malung studies (1.0 mm) and in the Blackhawk Island study (0.1 mm). This difference may have affected the decomposition rate by creating different environmental conditions. However, in a comparison carried out at the Blackhawk Island site, it was found that mass loss rates were similar for litter in bags with 0.1 and 2.0-mm mesh sizes (ABER et al. 1984). Similarly, Scots pine needles incubated in Scots pine forests in Sweden were degraded at the same rate in bags with mesh sizes of 0.1 or 1.0 mm (MAJBRITT JOHANSSON, Swedish Univ. Agr. Sciences, personal communication). Because soil animals had an insignificant effect on decomposition rate at the Jädraås site (BERG et al. 1980) and because the fine-mesh bags used at the Wisconsin site did not allow the entry of large soil animals, we assume that we observed decomposition caused largely by microorganisms.

We compared our chemical analytical methods by applying both of them to several sets of fresh and partly decomposed litter. The concentration of solubles relative to total litter mass was 1 to 2 percentage units lower with water and ethanol extractions (Swedish samples) than that with dichloromethane water extractions (Wisconsin samples). Also, the concentration of lignin was about one percentage unit lower when using the method of BETHGE et al. (1971) than when using the method of EFFLAND (1977).

Chemical compositions of Swedish samples were not corrected for ash contents. However, ash concentrations of these samples were only 1 to 2 % (BERG et al. 1982a). Chemical compositions of the Wisconsin samples, on the other hand, are presented on an ash-free basis because the ash concentrations of these samples varied from 0.3 to 20.2 %.

We did not identify individual polymer carbohydrates but have used the terms "holocellulose" to include all insoluble polymer carbohydrates, both cellulose and hemicelluloses, and "lignocellulose" for the sum of holocellulose and sulfuric-acid lignin. We are aware that it is not fully correct to use the term "lignin" for the sulfuric-acid-insoluble portion of litter in later stages of decomposition. However, we used it here for the sake of simplicity.

4. Results and discussion
4.1. Organic-chemical changes during decomposition

Of the lignocellulose constituents in decomposing litter, holocellulose begins disappearing sooner than lignin (BERG et al. 1982a). The early part of the holocellulose fraction to disappear is probably that part which was relatively unshielded by lignin. In any event, concentrations and absolute amounts of holocellulose decreased as decomposition proceeded, whereas concentrations of lignin increased. Such an increase has been followed in detail for Scots pine needle litter (BERG et al. 1982a) and birch leaves (BERG & WESSÉN 1984). In later stages of decomposition lignin concentrations became nearly constant (BERG et al. 1984). However, few studies of forest litter have continued long enough to note this phenomenon.

The lignin fraction, as defined by our analytical methods, includes both native lignin and recalcitrant compounds formed as decomposition proceeds. We are unable to detect transformations of lignin by our methods; we are only measuring net changes in concentration of acid-insoluble substances. Thus, the net changes in absolute amounts of lignin that we describe were due to both the decomposition of original lignin and the formation of recalcitrant acid-insoluble compounds. In litters, with high initial lignin concentrations (more than 30 %), the absolute amounts of lignin often start decreasing in very early stages of decomposition, whereas in litters with lower initial concentration of lignin, the absolute

amounts of lignin increase before a net decomposition begins. Studies with ^{14}C-labelled lignin (STOTT et al. 1983) suggest that lignin degradation can be rapid during early stages of decomposition, even if amounts of analytical lignin (acid-insoluble substance) do not decline.

As some holocellulose is structurally enclosed and shielded by, as well as chemically bound to, lignin (LUNDKVIST et al. 1980; NILSSON 1973), the lignin and holocellulose fractions cannot be completely decomposed independently of one another. In such late stages, when much of the remaining holocellulose is associated with lignin, both lignin and holocellulose should disappear at about the same rate (BERG et al. 1984).

The relative amounts of holocellulose in the insoluble fraction of litter can be defined by the fraction of holocellulose in lignocellulose. We termed this the holocellulose to lignocellulose quotient and designated it as "HLQ". HLQ-values decreased with increasing accumulated mass loss during the first 2 years of decomposition for all litters studied. In later stages of decomposition, the HLQ-values approached approximately constant values that differed among litter types (BERG et al. 1984).

4.2. Rate-regulating factors in late stages of decomposition
4.2.1. Definition of late stages

BERG & STAAF (1980b) and BERG et al. (1982b) suggested that the lignin loss rate strongly affects total mass loss rate in far-decomposed litters. Using this suggestion as a basis, we defined the late stage of decomposition as that which began when a net disappearance of lignin had started and when the litter was decomposed by at least 30%.

This rather arbitrary definition of late stages was chosen for 2 reasons. First, concentrations of solubles in the materials studied reached a fairly constant level after 30% of the initial mass was lost. Thus there will be a very small influence of soluble substances on mass-loss rates (BERG & ÅGREN 1984). Second, absolute amounts of the analytical lignin often increase during initial stages of decomposition. If lignin first increased and then decreased during an incubation period, the net change during that period would misrepresent the actual changes that had occurred.

4.2.2. HLQ and nitrogen concentration versus mass loss rate

A number of studies on decomposition of Scots pine needle litter at the Jädraås site, which had been followed into the late stages, provided data for an initial analysis of the effect of litter composition on mass loss rates in far-decomposed litters. The data set that was used covered several years with different climates, resulting in variable mass losses for the first year of incubation. In spite of that, it appeared meaningful to investigate the relationship. We plotted annual percentage mass losses during late stages of decomposition vs values for HLQ at the start of each one-year period and used data originating from different time periods in the 120-year-old Scots pine forest and an adjacent clear-cut area (Table 1). According to the definition of late stages (above), 25 sets of data from the old forest and four sets of data from the clear-cut area studies (sets L, M, O and P) were available (Table 1). The straight-line relation obtained for annual mass loss as a function of HLQ at the beginning of the period was highly significant ($r = 0,827$; $p < 0.001$; $n = 29$) (Fig. 1).

The HLQ-values used in these relationships ranged from 0.43 to 0.633. In far-decomposed litters, HLQ-values appeared to approach an asymptote or a minimum value (BERG et al. 1984).

Although we could extrapolate the linear relation to HLQ-values where decomposition rate would be close to zero, we expect that the HLQ-value would not decrease much below the asymptotic values previously described (BERG et al. 1984).

When litter is decomposed, its nitrogen concentration increases proportionally to accumulated mass loss (STAAF & BERG 1982; ABER & MELILLO 1980) and the percentage may increase by 3 to 4 times. KEYSER et al. (1978) and FENN et al. (1981) observed that even low levels of either ammonium or some amino acids repressed the formation of the lignolytic

Table 1. Annual losses for litter and lignin mass from far decomposed Scots pine needle litter and some leaf litters (Jädraås site) as well as values for holocellulose to lignocellulose quotients (HLQ) and concentration of nitrogen at the start of each one-year period (*cf.* Figures 1 and 2)

Time period	Litter type	HLQ	Nitrogen (%)	Loss in periof (%)		Ref.
				Litter	Lignin	
The old forest needle litters	Scots pine					
761110—771027	Set A	0.474	0.99	18.1	22,0	a
	Set B	0.561	0.71	26.7	13.3	b
	Set C	0.616	0.53	29.7	18.7	c
	Set 1 N0	0.618	0.42	33.4	12.8	c
	Set 1 N1	0.610	0.51	28.8	17.0	c
	Set 1 N2	0.589	0.67	27.5	18.6	c
	Set 1 N3	0.547	0.98	27.1	19.1	c
771027—781016	Set A	0.477	1.18	21.0	20.0	a
	Set D	0.610	0.56	29.5	9.3	c
	Set 2 N0	0.569	0.58	27.5	12.7	c
	Set 2 N1	0.561	0.59	25.6	11.5	c
	Set 2 N2	0.547	0.77	28.0	15.3	c
	Set 2 N3	0.526	1,12	26.2	14.8	c
781016—891107	Set D	0.516	0.82	22.7	17.7	b
	Set E	0.588	0.60	31.8	30.1	b
	Set 2 N0	0.492	0.82	22.5	19.2	b
	Set 2 N1	0.500	0.87	20.5	15.7	b
	Set 2 N2	0.477	1.18	17.2	15.3	b
	Set 2 N3	0.464	1.39	15.7	17.0	b
791107—801030	Set D	0.481	1.06	19.0	n,d,	b
	Set E	0.569	0.78	26.4	n.d.	b
	Set 2 N0	0.474	1.13	17.9	12.1	b
	Set 2 N1	0.469	1.11	20.4	17.5	b
	Set 2 N2	0.464	1.31	26.9	22.9	b
	Set 2 N3	0.471	1.53	18.2	13.8	b
Leaf litters 781016—791107	Birch leaves	0.471	1.23	14.4	12.0	d
	Cowberry leaves	0.432	1.12	15.1	14.0	e
	Heather hoots	0.468	1.27	15.2	14.6	e
The clear-cut area needle litters	Scots pine					
770514—780522	Set L	0.607	0.61	20.2	16.7	e
771027—781016	Set M	0.464	2.01	7.5	0.0	e
780522—790530	Set O	0.464	2.00	11.7	6.7	e
770914—781016	Set P	0.495	2.51	12.1	6.4	e

Key to references: a — BERG *et al.* (1982a); b — BERG & ÅGREN (1984); c — BERG & STAAF (1980b), d — BERG & WESSÉN (1984); e — BERG (1981).

enzyme system in some fungi and consequently lignin degradation became slower. However, this may not be a general phenomenon as some fungi can degrade lignin in cultures containing high nitrogen concentrations (JANSHEKAR *et al.* 1982; REDDY 1984). Although these were laboratory studies, they could have application to litter in the field and it is possible that litter decomposition is retarded by repression of the ligninolytic enzymes system, even if it is not an operative mechanism in all fungal species. Furthermore, NÖMMIK & VAHTRAS (1982) concluded that reactions take place between either ammonium or the amino group in amino acids and phenolic groups in lignin or lignin remains. Recalcitrant complexes thus formed should have a rate-retarding effect. Based on this BERG *et al.* (1982b) suggested a relation between high nitrogen levels in litter and low decomposition rates of lignin and litter.

Far-decomposed litters had higher nitrogen levels than those less decomposed, and thus nitrogen concentrations could add a further rate-decreasing effect to that caused by the
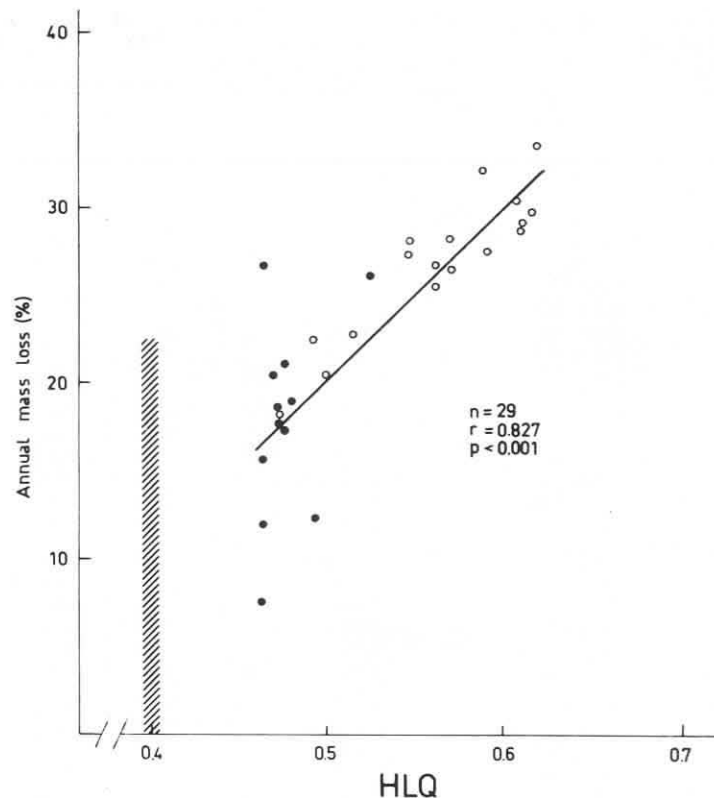
Fig. 1. Annual mass loss from Scots pine needle litter in later stages of decomposition (>1 year) (Jädraås site) as dependent on holocellulose to lignocellulose quotient (HLQ) at the start of each one-year period. (○) nitrogen concentration $<1\%$, (●) nitrogen concentration $>1\%$. The lower limit or asymptote for HLQ as described by BERG et al. (1984) is indicated. Data are included in table 1.

lower HLQ. Even if most of the nitrogen in far-decomposed litter is not in the form of ammonium or amino acids, the fact that nitrogen concentration is higher means that decomposition of a certain amount of organic matter is more likely to release a greater amount of ammonium and partly degraded proteins which then could exert a rate-retarding effect. We also found a proportionality between concentration of total nitrogen and the concentration of extractable ammonium in litter (BERG, unpublished). Using Scots pine needle litter we calculated the linear regression between concentrations of total nitrogen at the start of various one-year periods and the mass losses for the same periods. The result was a highly significant negative linear relation ($p < 0.001$) (Fig. 2, data in Table 1).

When a multiple linear regression was calculated with these data nitrogen concentration was the first factor to enter with $r = -0.861$ which was improved to 0.910 by the inclusion of HLQ (Table 2). Both factors were highly significant alone and in combination ($p < 0.001$). We tested for a possible interaction effect between nitrogen concentration and HLQ by including the factor N X HLQ which, however, added very little to the multiple correlation coefficient and was not significant.

The chemical changes discussed (i.e. increases in nitrogen concentration and decreases in HLQ) take place simultaneously. For Scots pine needles we consequently had litter with relatively high HLQ-values (>0.5) and relatively low nitrogen levels ($<1.0\%$) or vice versa. Both factors may be acting simultaneously to retard the decomposition process to a greater extent in the latter case than in the former.
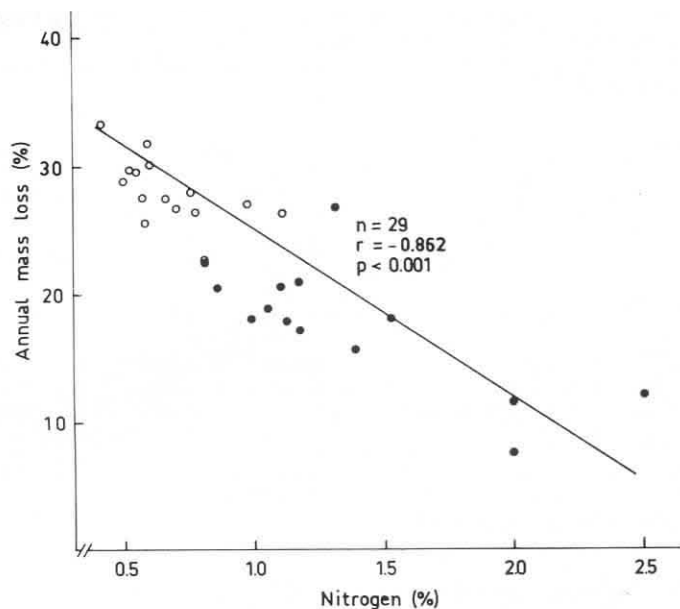
Fig. 2. Annual mass loss from Scots pine needle litter in later stages of decomposition (>1 year) (Jädraås site) as dependent on nitrogen concentration at the start of each one-year period. (○) holo-cellulose to lignocellulose quotient (HLQ) > 0,5; (●) HLQ < 0.5.
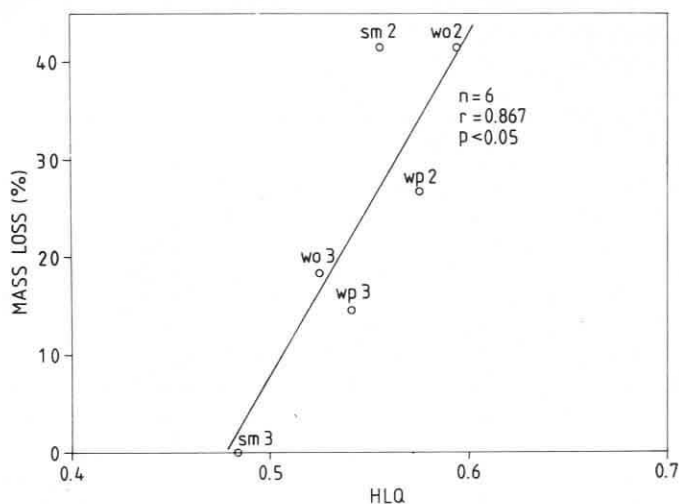

Fig. 3. Mass loss vs. holocellulose to lignocellulose quotient (HLQ) for there foliage litters in late stages of decomposition incubated at the Blackhawk Island site. SM: sugar maple leaves, WP: white pine needles, and WO: white oak leaves. The numbers 2 and 3 refer to second and third years of decomposition.

During decay of the litters we studied, the HLQ approaches a nearly constant value in the range of 0.4 to 0.5 whereas nitrogen concentration continues to increase. Thus, when HLQ becomes nearly constant and nitrogen concentration continues to increase, we may speculate that nitrogen concentration or factors related to it will emerge as the more important rate-regulating factors (cf. Fig. 1).

Table 2. Linear regression for mass and lignin loss rates in late decomposition stages as dependent on nitrogen concentration and holocellulose to lignocellulose quotient (HLQ)

Scots pine needles

Litter mass

Mass loss vs. HLQ	r =	0.827	n = 29	p < 0.001
Mass loss vs. N conc	r =	—0.861	n = 29	p < 0.001
Mass loss vs. HLQ and N conc	r =	0.910	n = 29	p < 0.001

Lignin mass

Mass loss vs. N conc	r =	—0.572	n = 27	p < 0.001

All litter types

Litter mass

Mass loss vs. HLQ	r =	0.852	n = 32	p < 0.001
Mass loss vs. N conc	r =	—0.840	n = 32	p < 0.001
Mass loss vs. HLQ and N conc	r =	0.914	n = 32	p < 0.001

Lignin mass

Mass loss vs. N conc	r =	—0.620	n = 30	p < 0.001

Note: The litter types used are those listed in Table 1.

4.2.3. Nitrogen concentration and HLQ versus lignin loss rate

The discussion so far deals with whole litter but we also investigated annual mass loss of lignin as dependent on nitrogen concentration. Using data for litter from the Jädraås sites, we plotted lignin mass loss *vs* nitrogen concentration at the beginning of the same period during the late stages of decomposition as previously defined. Using the needle litter data from the Jädraås site (Table 1) we found that lignin mass loss was significantly and negatively correlated with nitrogen level (p < 0.01) and that using all the data from this site improved the relation (p < 0.001; Table 2).

4.2.4. Test of the model with needle litters and leaf litters from more nutrient-rich sites

Having developed the model described above, we investigated its general validity by analyzing 3 other forest systems. The first 2 systems consisted of 4 sets of experimental plots of Scots pine and lodgepole pine monocultures (Malung sites) on a more nutrient-rich soil than that of the Jädraås site. We first tested the data set (Table 3) for the Scots pine forest and found that mass loss rates declined significantly with decreasing HLQ-values (p < 0.001) (Table 4). Also, the relation between mass loss rate and nitrogen concentration was highly significant. Multiple regression did not improve the relation.

The corresponding relations were then run for the lodgepole pine forests. Mass loss rate *vs* HLQ gave a significant relation which, however, was not as good as that for Scots pine needles. This may be due to the fact that the lignin concentrations were comparatively high in lodgepole pine needles even initially and did not change much during decomposition (BERG & LUNDMARK 1985). The relation between mass loss rate and nitrogen concentration had a higher level of significance (p < 0.01; Table 4). Multiple regression did not improve the relation. Because these plots were located particularly close to each other and the ground climate was about the same in the 8 stands, we combined the data sets for Scots pine and lodgepole pine. The combined sets were highly significant for mass loss *vs* HLQ and *vs* nitrogen concentration. The relation was not improved by multiple regression.

Having validated our model for both Scots pine and lodgepole pine needle litters incubated on the somewhat more nutrient-rich Malung sites, we next wanted to determine the applicability of the model for a variety of leaf litters in more mesic, nutrient-rich sites. For this purpose we used decomposition data for the 3 species of foliage litters incubated as Blackhawk Island which had statistically significant differences in mass loss between

Table 3. Annual losses of litter mass from far-decomposed Scots pine (SP) and lodgepole pine (LPP) needle litters (Malung sites) as well as values for holocellulose to lignocellulose quotients (HLQ) and concentrations of nitrogen at the start of each one-year period

Time period	Site number and litter type	HLQ	Nitrogen (%)	Litter mass loss in period (%)
790522—800519	1 LPP	0.550	0.48	37.9
	1 SP	0.602	0.62	39.5
	2 LPP	0.574	0.49	35.0
	2 SP	0.606	0.46	39.3
800519—810524	1 LPP	0.548	0.86	39.6
	1 SP	0.537	1.05	30.2
	2 LPP	0.546	0.72	23.3
	2 SP	0.522	0.90	25.3
810524—820526	1 LPP	0.481	0.96	3.8
	1 SP	0.456	1.33	16.7
	2 LPP	0.552	1.00	17.3
	2 SP	0.473	1.01	13.4
791029—801029	1 LPP	0.529	0.51	35.0
	1 SP	0.599	0.68	37.4
	2 LPP	0.550	0.51	38.7
	2 SP	0.558	0.49	35.6
	3 LPP	0.557	0.49	39.4
	3 SP	0.565	0.60	34.9
	4 LPP	0.557	N.D.[a]	31.5
	4 SP	0.555	N.D.[a]	35.9
801029—811027	1 LPP	0.526	0.68	21.4
	1 SP	0.476	0.87	12.4
	2 LPP	0.503	0.97	22.2
	2 SP	0.483	0.83	24.0
	3 LPP	0.481	0.96	20.1
	3 SP	0.479	0.98	26.3
	4 LPP	0.491	N.D.[a]	32.7
	4 SP	0.490	N.D.[a]	10.6
811027—821021	1 LPP	0.480	0.93	32.7
	1 SP	0.446	1.01	20.9
	3 LPP	0.502	1.20	13.8
	3 SP	0.458	1.20	16.1

Note: Site number and data from BERG & LUNDMARK (1985).
[a] N.D. = not determined.

Table 4. Linear regressions for mass loss rates in late stages of decomposition as dependent on nitrogen concentration and holocellulose to lignocellulose quotient (HLQ) at the Malung sites

Scots pine needles
| Mass loss vs. HLQ | r = 0.885 | n = 16 | p < 0.001 |
| Mass loss vs. N conc | r = —0.790 | n = 14 | p < 0.001 |

Lodgepole pine
| Mass loss vs. HLQ | r = 0.534 | n = 16 | p < 0.05 |
| Mass loss vs. N conc | r = —0.724 | n = 14 | p < 0.01 |

Scots pine and lodgepole pine needle litter
Mass loss vs. HLQ	r = 0.727	n = 32	p < 0.001
Mass loss vs. N conc	r = —0.743	n = 28	p < 0.001
Mass loss vs. HLQ and N conc	r = 0.725	n = 32	p < 0.001
Mass loss vs. HLQ and N conc and HLQ×N	r = 0.798	n = 32	p < 0.001

Noote: Needle litter types used were lodgepole pine and Scots pine.

samplings (ABER *et al.* 1984). Following the procedure used for the Swedish litters (Fig. 1), we plotted percent mass loss as a function of the HLQ at the beginning of each mass loss period (Fig. 3).

The 3 litters had a decline in both HLQ and mass loss rate and were thus in agreement with the model. For these 3 litters, mass loss rate was correlated with HLQ at the beginning of each incubation period ($r = 0.870$; $n = 6$; $p < 0.05$).

For the pine needle litters of the Jädraås and Malung sites, we found that decay rates were inversely correlated with the concentration of nitrogen during late stages of decay. The relationship between nitrogen concentration and decay rate was less clear for the Blackhawk Island litters. White pine needles and white oak leaves had a decline in percentage mass loss at higher nitrogen concentrations. Sugar maple leaves, in contrast, had a decrease in both nitrogen concentration and decay rate, with no significant mass loss during the third year of incubation. Sugar maple litter did not conform to our model perhaps because it had reached a very late stage of decay (as evidenced by its lack of measurable mass loss and a relatively high nitrogen-mineralization rate) and had therefore fallen outside the region for which our model is valid. On the other hand, the deviation noted for sugar maple is based on a single pair of data points and is hardly a basis on which to dismiss the model. Thus, the Blackhawk Island data agreed well with our model for the rate-regulating role of HLQ, but not entirely for the role of nitrogen.

We finally calculated a linear regression using all the pine needle litter data from the 4 systems and obtained highly significant relations for annual mass loss *vs* HLQ ($r = 0.674$; $n = 63$; $p < 0.001$). Mass loss *vs* nitrogen concentration also gave a highly significant relation ($r = 0.711$; $n = 59$; $p < 0.001$) which improved in a multiple regression analysis ($r = 0.764$; $n = 59$; $p < 0.001$).

In conclusion, it appears that the relations suggested may have a validity for litter in pine forest systems, and, although we had a smaller data base for other systems, it appears safe to draw the conclusion that it has a validity applicable to deciduous systems.

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6. References

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Synopsis: *Original scientific paper*

McCLAUGHERTY, C., and B. BERG, 1987. Cellulose, lignin and nitrogen concentrations as rate regulating factors in late stages of forest litter decomposition. Pedobiologia 30, 101—112.

Mass loss and changes in chemical composition during the decay of a variety of forest litters decomposing at several very different sites were measured. The data were used to examine general factors that regulate patterns and rates of decay in late stages of decomposition. The fraction of holocellulose in lignocellulose, termed the holocellulose to lignocellulose quotient (HLQ), is presented as an index for describing the relative amount of readily available carbon during decay. In later stages of decomposition, the HLQ was positively correlated with litter mass loss rates, and as the HLQ-values declined during decomposition, mass loss rates also declined. There was also a negative linear relationship between nitrogen concentrations and mass loss rates in later stages. These findings are discussed relative to the physiology of litter degrading microorganisms.

Key words: litter, litter decomposition, lignin decomposition, nitrogen, substrate quality.